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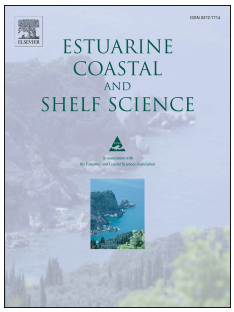

Comparing the network structure and resilience of two benthic estuarine systems following the implementation of nutrient mitigation actions

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Comparing the network structure and resilience of two benthic estuarine systems following the implementation of nutrient mitigation actions.

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Key words: Comparative studies, Ecopath with Ecosim, Estuary, Eutrophication, Network analysis.

Abstract

The structure and resilience of benthic communities in coastal and estuarine ecosystems can be strongly affected by human mediated disturbances, such as nutrient enrichment, often leading to changes in a food webs function. In this study, we used the Ecopath model to examine two case studies where deliberate management actions aimed at reducing nutrient pollution and restoring ecosystems resulted in ecological recovery. Five mass-balanced models were developed to represent pre and post-management changes in the benthic food web properties of the Tamar (1990, 1992, 2005) and Eden (1999, 2015) estuarine systems (UK). The network functions of interest were measures related to the cycling of carbon, nutrients and the productivity of the systems. Specific attention was given to the trophic structure and cycling pathways within the two ecosystems. The network attribute of ascendency was also examined as a proxy for resilience and used to define safe system-level operating boundaries. The results of the resilience metrics ascendancy (A) and its derivatives capacity (C) and overhead (O) indicate that both systems were more resilient and had higher resistance to potential stressors under low nutrient conditions. The less perturbed networks also cycled material more efficiently, according to Finns cycling index (CI), and longer cycling path lengths were indications of less stressed systems. Relative Ascendency (A/C) also proved useful for comparing estuarine systems of different sizes, suggesting the Tamar and Eden systems network structures have remained within their pre-defined "safe operating zones". Overall, this analysis presents justification that efforts to reduce nutrient inputs into the Tamar and Eden estuaries have had a positive effect on the trophic networks of each system. Moreover, the consensuses of the network indicators in both systems suggest ecological network analysis (ENA) to be a suitable methodology to compare the recovery patterns of ecosystems of different sizes and complexity.

1 Introduction

There is a growing need to manage ecosystems sustainably so that they can continue to deliver the goods and services on which society depend (Beaumont *et al.,* 2007; Bennett *et al.,* 2015; Costanza *et al.,* 2017). This is particularly the case for coastal marine systems where increasing population pressure, urbanisation and nutrient run-off from the coastal zone has increased the number of large-scale impacts affecting estuarine systems (Dolbeth *et al.,* 2011; Ellis *et al.,* 2015). As a consequence, there is a growing movement towards an integrated 'Ecosystem-based' approach to management, which focuses on how individual actions affect whole ecosystems, rather than considering these impacts in a piecemeal manner (Leslie, 2018). One alternative method to considering the organisms within ecosystems as an aggregate property, is to consider the emergent properties of the whole ecological system rather than of any of its individual components. Exergy, a thermodynamic concept, has been applied in ecology since the 1970's and is defined as the amount of work a system can perform when it is brought to thermodynamic equilibrium with its environment (Jørgensen & Mejer, 1977; 1979). Compatibly, ecological network analysis (ENA) can extract comprehensive information on the flow and cycling of matter from mass-balanced flowcharts, including trophic structure and transfer efficiencies, and the organisation or resilience of the food web (Field *et al.,* 1989, Gaedke, 1995). Taken together, these methodologies have a long legacy in assessing ecosystem health and in analysing complex interactions within marine ecosystems (Odum, 1953; 1969; 1996; Ulanowicz, 1986; 1997; 2012) with several ENA tools now available within a number of easily accessible software packages including NETWRK4 (Ulanowicz & Kay, 1991), WAND (Allesina & Bondavalli, 2004), Ecopath with Ecosim (Christensen & Walters, 2004) and R (Laua *et al.,* 2015).

Perhaps the most commonly used and emerging example of this type of modelling approach is the Ecopath with Ecosim (EwE) modelling software (Christensen *et al.,* 2005), which has over 400 models published to date (Colléter *et al.,* 2015), and is the most applied tool for modelling marine and aquatic ecosystems globally. EwE models have a number of ENA features and can been selected to: identify and quantify major energy flows in an ecosystem, interactions between species, compare coastal ecosystems of different sizes, evaluate the effects of climate induced or anthropogenic variability on ecosystems, explore management policy options. EwE models have also been applied in testing ecosystem theories on eutrophication (Patricio *et al.,* 2006; Baeta *et al.,* 2011; Vasslides *et al.,* 2017), resilience, stability and regime shifts (Pérez-España & Arreguín-Sánchez, 2001; Tomczak *et al.,* 2013; Arreguín-Sánchez & Ruiz-Barreiro, 2014; Heymans & Tomczak, 2016). Thus, the aim of this paper was to use the Ecopath software with ENA analysis to examine and compare the network system attributes of two temperate UK estuaries, the well-document Tamar Estuary, in south-west England and the smaller less well studied Eden Estuary, in north-east Scotland. Both systems have gone through extensive periods of ecological change over the last thirty years, as a result of a shift towards an agriculture production policy option in the Eden catchment (1999-2015) and a combination of water quality improvement initiatives in the Tamar Estuary (1990-2005), allowing the representation of eutrophic and post-eutrophic states. Therefore, five mass-balanced models were developed using the "Ecopath with Ecosim" software package for the years 1990, 1992 and 2005 (Tamar) and 1999 and 2015 (Eden) to assess changes in the benthic food web properties of the Tamar and Eden estuarine systems. Field, laboratory and literature information was used to construct the models. The main study objective was to assess the effects of:

(1) a pre-management period of excessive anthropogenic enrichment, which led to excessive production of organic matter in the form of algal blooms and localised hypoxic symptoms (Tamar 1990);

(2) a pre-management period with high nutrient levels (Tamar 1992; Eden 1999);

(3) a post-management period after the implementation of mitigation measures following long periods of hypernutrification (Tamar 2005; Eden 2015).

2.1 A brief description of the ecosystems

Tamar Estuary (50021' N, 004010' W).

The Tamar estuary is a medium sized (31 km-long) estuary situated on the border between Cornwall and Devon on the south-west coast of England (Figure 1). The estuary itself comprises a complex of marine inlets (rias) stretching from Gunnislake weir (upper tidal limit) to Plymouth Sound (lower tidal limit) (Money *et al.,* 2011). Together, the Tamar Estuaries Complex (encompassing the River Lynher and St John's Lake in addition to the Tamar–Tavy, and hereafter referred to as the Tamar estuary) and Plymouth Sound, are designated as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (92/43/EEC) and a Special Protected Area (SPA) under the European Commission Directive on the Conservation of Wild Birds (79/409/EEC). The many different habitats within the Tamar estuary, have been studied intensively for more than a century by researchers of the Marine Biological Association (MBA), University of Plymouth (UoP) and Plymouth Marine Laboratories (PML), who have conducted numerous hydrographic, chemical and biological surveys in the Western English Channel, including Plymouth Sound and Tamar estuary (see Southward & Roberts, 1987 for historical perspective). As a result, the Tamar estuary and its surrounding waters is one of the best documented estuarine complexes in the UK and is ideally suited to conducting seascape-scale or systems-based research.

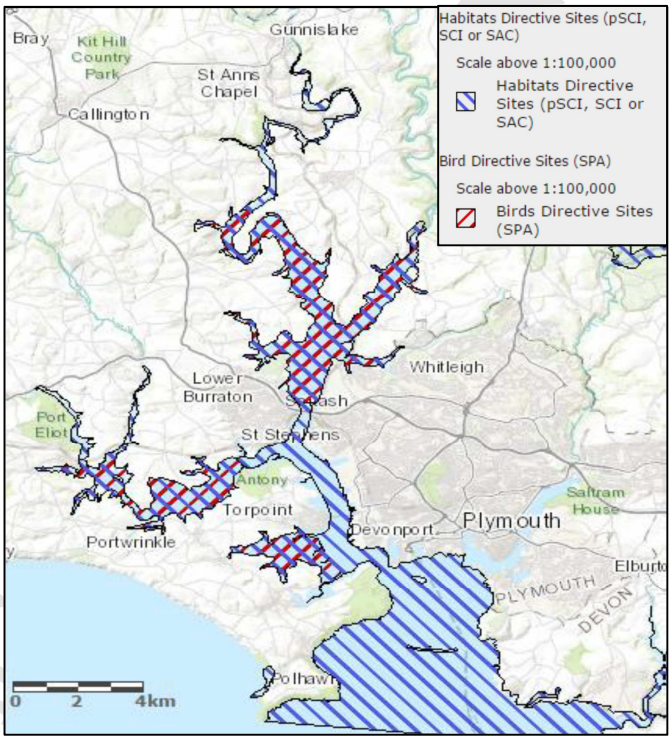


Figure 1: Map of the Tamar Estuary and Plymouth Sound European Marine Site.©Copyright European Environment Agency (EEA)

In common with many British estuaries, from the 1980s to the early 1990s, the Tamar experienced significant nitrogen and phosphorous enrichment due to excessive agricultural run-off due to land use changes in the upper catchment (Knox *et al.,* 1986), while sewage discharges constituted localised chronic contamination and nutrient-associated water quality problems in the lower estuary (Morris *et al.,* 1981; 1986; Readman *et al.,* 1986). As a result during these periods the system was considered eutrophic, with respect to nitrogen under criteria proposed by Dodds *et al.* (1997) (>1.5

mg/L^{-1}) and the EU guideline of 9 (µg/L^{-1}) for the protection of course freshwater fish, but not considered polluted in terms of nitrogen according to criteria under the Nitrates Directive (>5.65 mg/L^{-1}) for official designation as a eutrophic system (Table 1). This culminated during the period of 1990 when low river flows, high water residence times and high nutrient concentrations in the form of phosphorous compounds, interrupted upstream communication with the upper portion of the system, resulting in large blooms of benthic microalgae and increased biomass of macroalgae across the estuary. The resultant conditions included widespread salmonid fish deaths caused by localized areas of low oxygen conditions (Darbyshire, 1996; Harris, 1988; 1992), in addition to relatively low pHs and high suspended solids (trapped in the upper estuary following spring tides), leading to reported changes in biodiversity and functioning of the system. During this period annual reactive phosphorous concentrations exceeded 100 (µg/L) and the Tamar was officially classed as eutrophic using interim standards set by the Environment Agency (EA, 1998). Following a recovery period the following year, in 1992 various management efforts such as the "New South West – Clean Sweep and Beyond project" and the "Plymouth Urban Diffuse Pollution Project" were put in place to clean up nutrient related issues across the estuary. As a result, much of the eutrophic symptoms associated with the early 1990's had subsided by the early 2000's. For example average reactable phosphorus concentrations were shown to decrease from 1990 levels of 110(µg/L^{-1}) to 63(µg/L^{-1}) for the period of 1992 and to an even lower 47 (µg/L) by 2005 (Mankasingh, 2005).

Table 1: Summary of annual average concentrations of environmental variables for the Tamar Estuary (1990-2005).

Variable/Year	1990	1992	2005	Source
Ammonium (mg l^{-1})	0.07	0.04	0.02	Mankasingh, (2005)
Biochemical oxygen demand (mg l^{-1})	2.11	1.52	1.10	Environment Agency
Chlorophyll *a* (mg l^{-1})	29.55	6.98	6.32	Environment Agency
Dissolved oxygen (mg l^{-1})	10.00	10.76	10.29	Environment Agency
Filterable reactive phosphorous (µg l^{-1})	110	63	47	Mankasingh, (2005)
Nitrate (mg $^{l-1}$)	11.65	12.10	12.61	Mankasingh, (2005)
Nitrite (mg l^{-1})	0.03	0.02	0.008	Mankasingh, (2005)
pH	6.33	7.70	7.59	Environment Agency
River flow ($m^{-3/-s}$)	3.48	8.65	4.01	The National River Flow Archive (NRFA) Gunnislake gauging station.
Surface salinity (ppt)	17.56	16.30	16.91	Environment Agency
Temperature(°C)	12.10	11.08	11.95	Environment Agency

Eden estuary (56022' N, 2050' W)

In comparison with the Tamar, the Eden Estuary is a small (11km-long) shallow bar built or 'pocket' estuary, located between the village of Guardbridge and the town of St Andrews on the East coast of Scotland (Figure 2). Collectively the Eden estuary along with the Firth of Tay Estuary is designated as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (92/43/EEC) and a Special Protection Area (SPA) under the European Commission Directive on the Conservation of Wild Birds (79/409/EEC). The main channel of the estuary is flanked by relatively wide intertidal areas (8km^2) that plays host to large populations of overwintering waterfowl and wading bird species. Historically the intertidal mud and sand flats of the estuary have been sampled intensively by researchers from the University of St Andrews, with many studies undertaken from of the Gatty

Marine Laboratory (Bennett & McLeod, 1998) providing a robust baseline from which to draw comparisons.

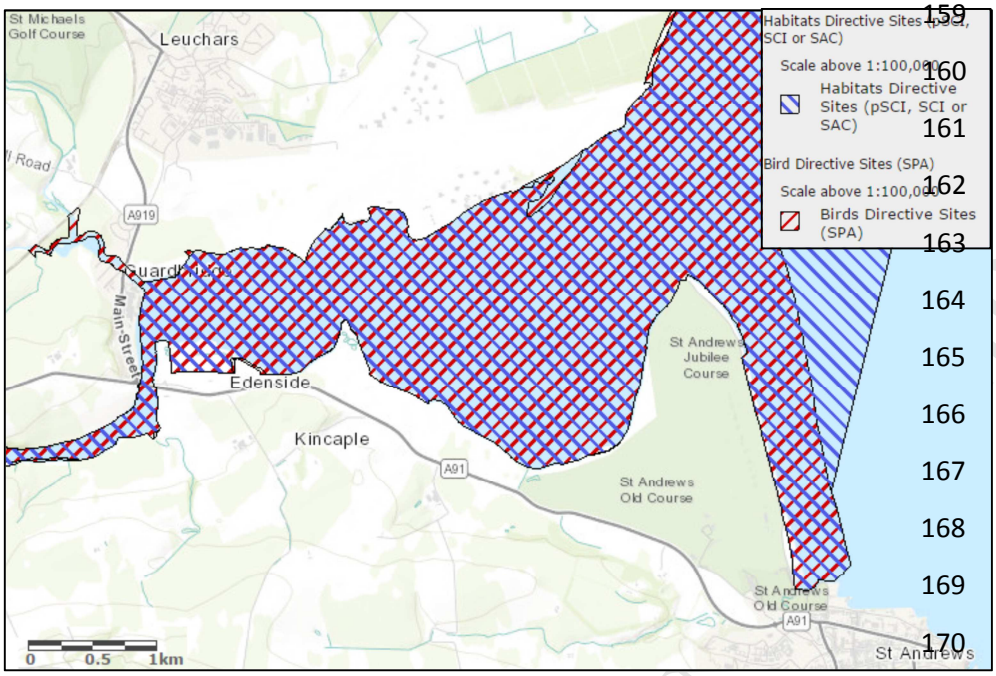


Figure 2: Map of the Eden Estuary European Marine Site. ©Copyright European Environment Agency (EEA).

Anthropogenic pressure in the form of increased nutrients from arable and livestock production is one of the most significant pressures influencing the Eden with high levels of nitrogen compounds entering the estuary *via* the river Eden (Clelland, 1997). Historically this has led to a number of ecological problems such as the closure of mussel beds as unfit for human consumption and widespread fish mortalities (Defew & Paterson, 2009). As a consequence the catchment was designated as a nitrate vulnerable zone in 2003 (SEERAD, 2003). Nutrient inputs are now in decline (Table 2) thanks to increased legislation resulting from the Nitrates Directive (NVZ) and Sensitive Area (UWWTD) designations (Macgregor & Warren, 2015), including an upgrade of the Guardbridge sewage treatment works in 2008 and the closure of the Guardbridge paper mill and adjacent pig farm with their associated effluent.

Table 2: Summary of annual average concentrations of environmental variables for the Eden Estuary (1999-2015).

Variable /Year	1999	2015	Source
Ammonium (mg l^{-1})	0.091	0.048	Environment Agency
Chlorophyll *a* (mg l^{-1})	10.56	4.28	Environment Agency
Dissolved oxygen (mg l^{-1})	11.39	10.74	Environment Agency
Filterable reactive phosphorus (mg l^{-1})	0.23	0.098	Environment Agency
Nitrate (mg l^{-1})	7.72	5.82	Environment Agency
Nitrite (mg l^{-1})	0.035	0.015	Environment Agency
pH	7.92	8.11	Environment Agency
River flow ($m^{-3}/^{-s}$)	2.67	2.13	The National River Flow Archive (NRFA) Kemback gauging station.
Temperature (°C)	9.45	10.10	Environment Agency

2.2 Materials & Methods

Biomass flow networks (t/km^2/yr^{-1}) were constructed for the systems outlined above, using the "Ecopath with Ecosim" software package (v6.5) for the years 1990, 1992 and 2005 (Tamar) and 1999 and 2015 (Eden) representing eutrophic and post-eutrophic systems. Ecopath trophic models are mass balance models that create a static snapshot of energy flows and there interactions in an ecosystem represented by trophically linked biomass 'pools' or ecological guilds of species (Pauly *et al.,* 2000). In a model, the energy input and output of all living groups must be balanced. Ecopath parameterizes models based on two master equations one to describe the production term and one for the energy balance of each group (Christensen *et al.,* 2005). The first equation divides the production of each compartment into individual components. This is implemented with the equation:

Production = total fishery catch rate + predation mortality + biomass accumulation + net migration + other mortality

Or, more formally,

$$\mathrm{B_i\,x}\left(\frac{P}{B}\right)i\ EE_i - \sum_j \left(B_j x\left(\frac{Q}{B}\right)j\ x\ DC_{ij}\right) - Y_i - BA_i - E_i = 0 \qquad \textbf{Equation 1}$$

Where B_i and B_j are the biomasses of prey (i) and predators (j) respectively; P/B_i the production/biomass ratio; EE_i the ecotrophic efficiency which describes the proportion of the production that is utilized in the system,; Y_i the fisheries catch per unit area and time; Q/B_j the food consumption per unit biomass of j; DC_{ji} the fraction of prey i in the average diet of predator j; BA_i the biomass accumulation rate for i (the default value of zero was used to indicate no biomass accumulation); and E_i is the net migration of i, calculated as immigration (migration into the area covered by the model) minus emigration (migration out of the area, the default value of zero was used). Within the model, biomass was expressed as tonnes km^{-2} and production and consumption as tonnes km^{-2} yr^{-1}.

Equation two expresses how the energy balance within each compartment is ensured when consumption by prey biomass = production + respiration + unassimilated food

Or, more formally,

$$B_i\left(\frac{Q}{B}\right)i = B_i\mathrm{x}\left(\frac{P}{B}\right)i + R_i + U_i \qquad \textbf{Equation 2}$$

where R_i is the respiration rate, and U_i the unassimilated food rate. Respiration is used in Ecopath, only for balancing the flows between groups and refers to the assimilated fraction of matter that is not used in production. Following other estuarine Ecopath models (e.g. Baeta *et al.,* 2011), it is assumed that autotrophs and detritus based organisms have zero respiration with all nutrients that leave the compartment being re-utilized. For each compartment unassimilated food (U_i) consists of food which is egested and flows to the detritus. Following Christensen *et al.* (2000), our models used a U_i default value of 0.20 for all groups (i.e. 20% of the consumption for all groups).

2.2.1 Sampling methods and data collection

Chlorophyll *a* measures provided by the Environment agency (Table 2) for each catchment were transformed into a proxy for phytoplankton biomass using a conversion factor taken from Anderson & Williams (1998). Quantitative biomass data for the main benthic primary producers (microphytobenthos, macroalgae and other macrophytes) at the estuarine scale were made using the Ecopath model based on case study specific estimates of their production, using data from small scale *in situ* measurements (e.g. Bale *et al.,* 2006) and knowledge of other trophic assemblages. Model biomass estimates were examined and compared with the existing literature to ensure the predations were plausible. For instance, there have been a number of long-term biotope and aerial surveys of saltmarsh and macroalgal extent (Webster *et al.,* 1998; EA., 2000; Widdows *et al.,* 2007; Curtis *et al.,* 2010) on various regions of the Tamar complex. The macroalgal group here is likely to comprise of locally registered species such as *Enteromorpha* and *Ulvae spp*. while the 'other' macrophyte grouping is likely to comprise a wide variety of seagrass and saltmarsh species such as by not limited to: common saltmarsh-grass (*Puccinellia maritime)*, common cord-grass (*Spartina anglica)*, common eelgrass (*Zostera marina)*, red fescue (*Festuca rubra)* and sea couch (*Elymus pycanthus)*.

To obtain an approximate value for microphytobenthic biomass and production in the Eden system, contact cores were taken across identical transects of each of the three main zones of the estuary in 1999 and 2015 by sampling the top 2 cm of the surface sediment (see Ford & Honeywill, 2002 for full protocols). The presence of macroalgae (biomass t km^2) was estimated by a survey of macroalgae within 5m radius of each sampling point (Ford & Honeywill, 2002). Macroalgae were mostly identified to be Enteromorpha and Ulvae *spp*. Estimates of 'other' macrophytes in the system were calculated, based on known *in situ* estimates of saltmarsh extent and production (Fife Council, 2008; Maynard, 2003; 2014; Maynard *et al.,* 2011). Common species represented by this grouping were likely to include common saltmarsh-grass (*Puccinellia maritime)*, sea clubrush (*Bolboschoenus maritimus)* and the eelgrasses (*Zostera augustifolia)*, (*Z. noltii)*, and (*Z. marina)*.

In the Tamar system, invertebrate data from three studies allowed some inter-comparisons to be made at the estuarine scale at similar times of the year, using similar sampling methodologies (Watson *et al.,* 1995; SWW Tamar Estuary sublittoral sediment survey 1992 & Sanders, 2008). In the Eden estuary, extensive surveys of invertebrate data were collected in 2015 through identical surveys to those carried out in 1999 by the BIOPTIS programme (Watson *et al.,* 2018). During this campaign three sampling grids were established across three transitional areas of the estuary (Appendix A). Invertebrate densities for both systems were converted to biomasses using case study-specific relationships (e.g., Dashfield & McNeill, 2014 Tamar & Biles *et al.,* 2002 Eden). Invertebrate species that were not naturally present in one of the years or sites or whose roles in the trophic network were unimportant (biomass < 0.01 t/km^2) were not taken into account.

Data on demersal fish species and epibenthic crustaceans could not be collected at the estuarine level in each system for practical reasons. However, historical fisheries-independent trawl surveys mainly undertaken by Russel (1973), McHugh *et al*. (2011) & Dando (2011) reveal a relative temporal consistency in the overall numbers of flatfish and epibenthic crustaceans in the Tamar estuary between historic (1970 & 1980) and contemporary (2009) trawls. Similar observations into the autecology of the brown shrimp (*Crangon crangon*) by Henderson *et al*. (1987; 1990) and later by Campos *et al*. (2008; 2009; 2012) across several British estuaries including the Tamar suggest a consistency in the population structure and phylogeography of this species over our study period. Therefore, given that the spatial structure of the demersal fish and caridean shrimp assemblage has remained relatively constant, similar biomass values for each of these taxa were used over the time periods. Data on fish populations in the Eden were also unattainable from the literature due to a paucity of fish monitoring surveys within the estuarine complex. Demersal fish biomass estimates were therefore estimated by Ecopath, based on P/B. Q/B and EE. Data on epibenthic crustacean numbers, most specifically the brown shrimp (*Crangon crangon*) were obtained as part of the aforementioned macrobenthic invertebrate data collection.

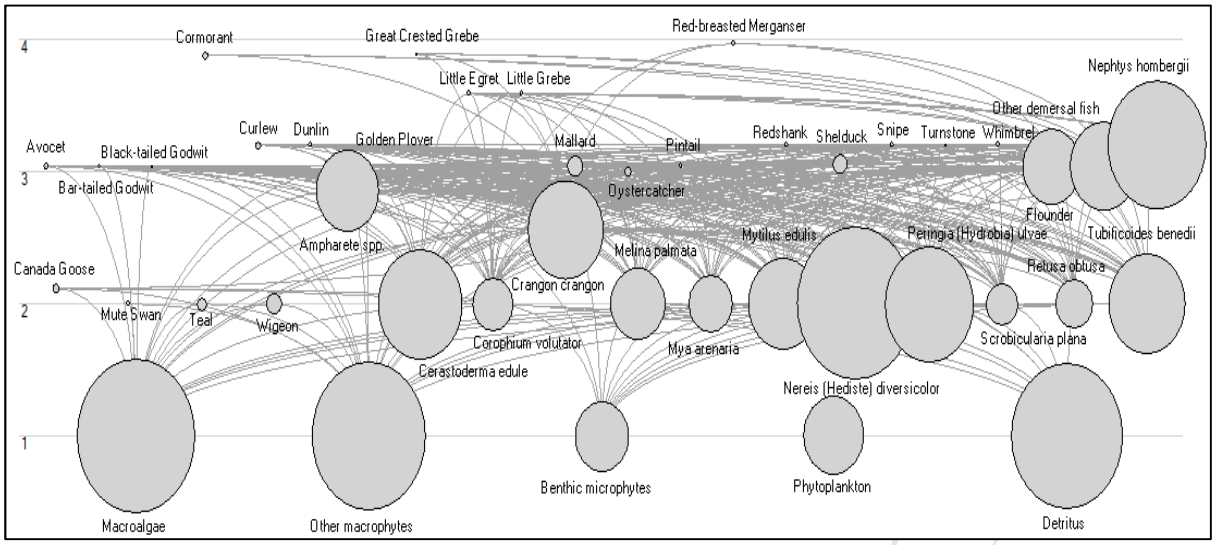
Population numbers for waterbirds in both systems were obtained for the period 1990-2015 from the WeBS (Wetland Birds Survey) database (Frost *et al.,* 2016). Bird counts were based on monthly observations across 15 (Tamar) & 5 sectors (Eden) covering the whole of each respective complex. Twenty-three waterbird species were selected from the Tamar system and Eighteen waterbird species from the Eden system (representing >95% of the total bird numbers in each system, with those excluded largely representing seabird species) from a list of local species known to inhabit and feed on the estuary recurrently, to increase the chance of interoperating temporal changes. Prior to analysis counts were converted to biomasses using species specific body weights outlined by Snow & Perrins (1998).

2.2.2 Compartments

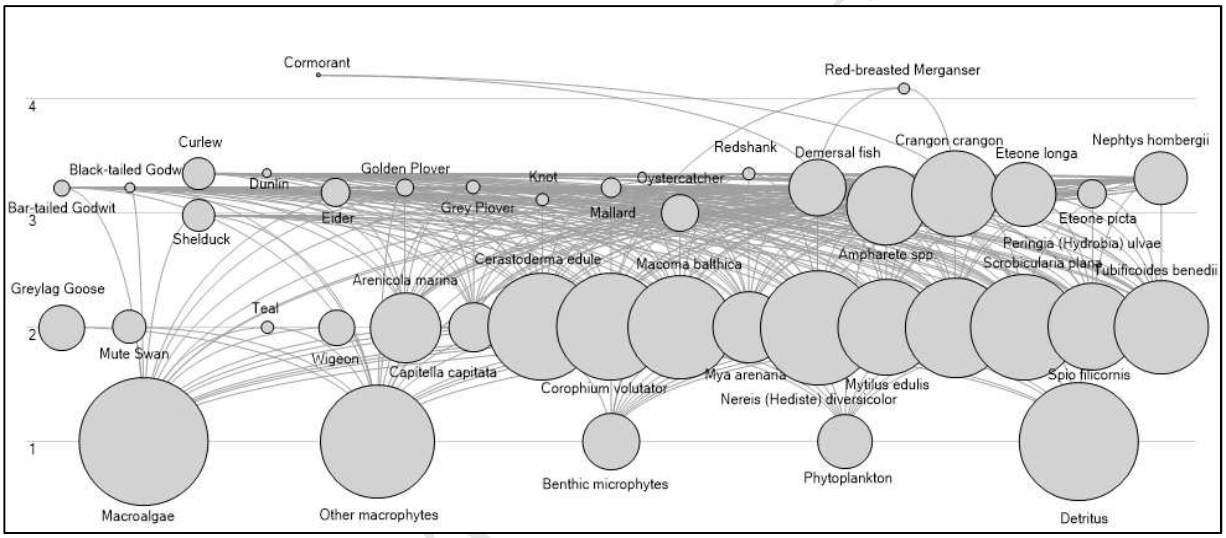
Some groups of species were grouped into compartments based on similar ecological niches. The benthic-microalgae group here is primarily composed of freshwater and marine diatoms with no single species dominating the community throughout the year. In the case of the Tamar, demersal fish species were amalgamated into one compartment comprising sole (*Microstomus kitt*), turbot (*Phrynorhombus norvegicus*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*). In the Tamar Estuary, the flounder (*Platichthys flesus)* was considered as a separate compartment being the only ray-finned demersal fish to migrate and colonize the upper reaches of the estuary due to its considerable powers of osmoregulation (Hartley, 1940; 1947). In the Eden Estuary, the demersal fish fish identity was assumed to be a combination of all benthic fish species know to occur within the estuary. In all models, invertebrate species belonging to family Ampharetidae were grouped together, with many of these species sharing a functional role. No data were available for bacteria, therefore the benthic bacterial biomass was considered has being part of the detritus compartment, as recommended by Christensen and Pauly (1992a, b).

2.2.3 Ecopath food webs and trophic structure

The final versions of the Tamar (Figure 3) and Eden (Figure 4) food webs comprised 43 and 41 taxa respectively, distributed over four trophic levels



297 **Figure 3** 2D representation of the food web from the Tamar Estuary (1990).



298 **Figure 4** 2D representation of the food web from the Eden Estuary (1999).

299 Whilst phytoplankton and benthic-microalgae are included due to their known importance in
300 structuring benthic ecosystems, other water column elements (zooplankton, planktivorous fish (e.g.
301 shad, sand eel) and their consumers (species in the family *Salmonidae*) were not included in this
302 model and are considered to follow a separate pelagic trophic pathway (Hall & Raffaelli, 1991). This
303 is due to both planktonic and benthic networks of cycling representing independent domains of
304 control (Baird & Ulanowicz, 1989), with benthic-microalgae constituting a significant proportion of
305 benthic estuarine ecosystem functioning. This model instead centres on a detritus based pathway
306 with particulate organic matter passing through micro-phytobenthos to macro-invertebrates to fish
307 or birds (e.g. Raffaelli, 2011) and a second pathway is also used from macroalgae to macro-
308 invertebrates or herbivorous wildfowl (Baird & Milne, 1981). In addition, although the harbour seal
309 (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) are known to roam freely through the Eden
310 Estuary (and to a lesser extent the lower Tamar Estuary), they were not included in either modelling
311 framework due to their diets mainly consisting of planktivorous fish (e.g. sandeels, whiting and
312 species of the family *Salmonidae*) foraged out with the estuarine area in question. For instance
313 Sharples *et al*., (2009), noted in a study of the diet of harbour seals in the Eden and adjacent St.
314 Andrews Bay to consist of 81 to 94% sandeels in winter and 63% in summer and autumn, with
315 salmonids making up the remaining prey captured.

316 **2.2.4 Production, consumption and diet composition**

317 Production/Biomass ratios required for Ecopath were collected from a number of web-based
318 databases (e.g., Fishbase (Froese & Pauly, 2016) and WeBS database (Frost *et al.,* 2016)). For all
319 vertebrate groups this information was readily available from these databases. For avian species,
320 production was calculated as recruitment (R) of young into the adult population in units per
321 individual (tonnes per year; Stenseth, 2002). For the primary producer and invertebrate groups,
322 Brey's (2001) Virtual Handbook on Population Dynamics, version 4 (Brey, 2012) was used to
323 calculate the P/B for all species. The weight-to-energy ratios needed in order to apply the empirical
324 method were also provided by Brey (2001). In the case of combined groups the means of each
325 component parameters, were weighted by the relative biomass of the components. For all
326 heterotrophic compartments, Production/ Consumption ratios were entered into the program in
327 order to estimate the Consumption /Biomass ratio's indirectly. The only exception was in the case of
328 demersal fish species where a holistic predictive model for Consumption/Biomass using asymptotic
329 weight, habitat temperature, a morphological variable and food type as independent variables were
330 calculated using Fishbase

331 Diet matrices were built for each taxa using information from a wide variety of literary sources and
332 summed to unity. Resident invertebrate diet compositions was compiled largely from MBA data
333 holdings including MARLIN and BIOTIC databases while shorebird and flatfish data referenced from
334 the WeBS and Fishbase databases respectively. Complimentary diet information was also gathered
335 from the literature (see Appendix B for all diet references). Initially all species were listed from each
336 taxa along with their percentage contribution to the compartment. Each observed dietary item was
337 then assigned to each individual group of species, with the final percentage of the diet assumed to
338 be proportional to the fraction that its biomass comprised of the total biomass of the functional
339 group.

340 **2.2.5 Anthropogenic exports (Yi)**

341 A complete mass balanced model needs estimates of the export rates from the system, including the
342 harvesting of economically important species. Commercial flat fishing mortality by means of landings
343 from the Tamar was considered sufficiently small enough to be negligible, based on records of
344 numbers of fish caught of species of 130 mm and upwards (Clark, 2012). Commercial fishing effort
345 on the Eden Estuary was also considered to be minor, with the estuary and surrounding St Andrews
346 Bay protected by a Scottish Inshore Fishing Order (1989) which forbids the use of all mobile fishing
347 gears, including trawling and dredging practices within the area. Similarly the harvesting of
348 commercial invertebrate species such as *Cerastoderma edule, Mytilus edulis, Hediste diversicolor,*
349 *Nephtys hombergii* and *Crangon crangon* for bait fisheries or human consumption was considered
350 insignificant in terms of overall biomass export from the system Tamar (Curtis, 2010) and Eden
351 where bait collection is strictly controlled.

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2.2.6 Pre-balancing analysis (PREBAL)

To add rigor and validity to the models a set of pre-balance diagnostics (PREBAL) outlined by Link (2010) and recommended by Heymans *et al.* (2016) were made to assess any issues with the models structure or quality of the primary input data. First the logarithmic ratios of biomass among various taxa groups were plotted (Appendix C) as they have been repeatedly identified as a major indicator of marine ecosystem functioning (Link, 2005; Mokany *et al.,* 2016). Generally biomass decomposition generally followed a sequential decrease moving across trophic levels. While detrital groups where not used it is noted for context that detrital standing stocks were on the same order of magnitude as primary producer biomass, consistent with systems such as estuaries and benthic orientated food webs that are particularly dependent upon detrital energy. In a second step, the vital rates of all taxa, in the form of Production/Biomass ratio and Consumption/Biomass ratio were plotted (Appendix C) for comparison, as these ratios are reflective of an amalgamation of an entire suite of physiological processes. As with the biomass estimates, there was an acceptable decline in vital rates with increasing trophic level.

2.2.7 Balancing the models

Using the ecological and thermodynamic rules for balancing Ecopath models outlined by Darwall *et al*., (2010) elements of the diet matrix or the values of the three inputted parameters were adjusted iteratively until all logical constraints were met. This was done starting with the lowest quality data first, preserving the most reliable data. In both the Tamar and Eden case studies, the most reliable data were the biomass and production values, and consequently these values were left largely unchanged. Diet matrices were principally unaltered but differed slightly to reflect the known trophic responses of species to different pressures. In all incidences the balancing parameter changes fell within the ranges of uncertainty associated the development of the 'pedigree'— a routine in Ecopath modelling that quantifies the quality of the input data by assigning confidence intervals based on the origin of the information. The pedigree index P calculated for the Tamar models was 0.481 and 0.593 for the Eden, with the higher latter value reflecting the use of locally collected data and trophic information used to parameterise the models. The various parameters for the balanced Ecopath models of the Tamar and Eden ecosystems are presented in (Appendix D).

2.2.8 Summary of system statistics and indices

After mass-balancing the models, a number of indices that describe the structure, function and resilience of each system as a whole were calculated using a suite of Ecological Network Analysis (ENA) algorithms incorporated into Ecopath (Christensen *et al.,* 2005). A summary of each index chosen is given in Table 3.

401

402 **Table 3 Selected Ecological Network Analysis (ENA) indicators**

403

System Indices	Description	Units
Sum of all consumption (Σ C),	Σ C is the sum of all consumption in a system.	t km^{-2} yr^{-1}
Respiratory flows (Σ R)	ΣR is the sum of all respiratory flows in a system.	t km^{-2} yr^{-1}
Flows to detritus (Σ FtD)	Σ FtD consists of what is egested (the non-assimilated food) and those elements of the groups, which die of old age, diseases, etc.	t km^{-2} yr^{-1}
Production (Σ P)	Σ P is the sum of all production flows in a system.	t km^{-2} yr^{-1}
Total system throughput (TST)	TST represents the entire amount of biomass flow within the system (consumption + export + flows to detritus + respiration) and represents the size of the system (Ulanowicz, 1986). As such, it is an important parameter for comparisons of trophic flow networks	t km^{-2} yr^{-1}
Total biomass (excluding detritus) (∑B)	Total biomass in the system excluding detritus.	t km^{-2}
Total primary production/total biomass (PP/B),	PP/B, is expected to be a function of the system's maturity (Odum, 1969).	The PP/B ratio can take any positive value and is dimensionless.
Primary production/respiration (PP/R)	PP/R, is the difference between total primary production and total respiration. It is considered by Odum (1971) to be an important ratio for description of the maturity of an ecosystem.	The PP/R ratio can take any positive value and is dimensionless.
Total throughput cycled (T cycled)	T cycled is the fraction of, an ecosystem's throughput that is recycled.	t km^{-2} yr^{-1}
Finn's index (CI)	CI captures the functions of carbon and nutrient cycling in the system using a proxy of (% of total throughput).	% of total throughput
Predatory cycling index (PI)	PI is a slightly modified form of the CI index, computed after cycles involving detritus groups have been removed.	% of throughput w/o detritus
Average path length (APL)	APL measures the average number of transfers a unit of medium (e.g. carbon) will experience from its entry into the system until it leaves the system (Baird *et al.,* 1991).	The APL is a positive value and is dimensionless.
The system omnivory index (SOI)	SOI specifies how consumer feeding interactions are distributed across trophic levels. A value close to 0 indicates the consumer is specialised (i.e. it feeds on one trophic level) while a higher value indicates a diet composed of prey across many trophic levels (Christensen *et al.,* 2000).	The SOI is a positive value and is dimensionless.
Ascendency (A)	A represents both the size and organisation of a system (Ulanowicz, 1986, 1997). Ascendency is a measure of a systems stability and a proxy for a systems resilience.	Flowbits or the product of flow (e.g., t/km^{-2}/year)
Development capacity (C)	C represents the upper limit for the size of the Ascendency. Both ascendency and capacity are measures of a systems stability and resilience.	Flowbits or the product of flow
System Overhead (O)	O is the difference between capacity and ascendency and is also a measure of system resilience. Higher system overheads indicate that a system has a larger amount of energy in reserve (in flowbits) with which it can use to resist impacts (Ulanowicz, 1986). Overhead is also defined as the pathway redundancy (Ulanowicz, 1997).	Flowbits or the product of flow

3 Results and discussion

3.1 Statistics of ecological functioning and network structure

To quantify the difference within and between the two systems it was necessary to compare the relative magnitude of change in their various system information indices (Table 4). One clear comparison between the networks is that the Tamar is far more active than the Eden, its total system throughput (23464 t km^{-2} yr^{-1}, 2005, defined as the sum of all flows in the system) is almost 25% larger than that of the Eden (17957 t km^{-2} yr^{-1}, 2015). Some of the higher activity in the Tamar can be attributed to its greater size and freshwater inputs than the Eden, but higher nutrient inputs to the Tamar are also likely to enhance its activity. Because total system throughput scales all information indices, the ascendency and other related variables are uniformly greater for the Tamar. Despite the topological network differences of each system, in both systems, Total biomass (excluding detritus) decreased substantially between the pre and post-management periods. The impact of these changes was reflected by falls in many of the system indices including: consumption, respiratory flows, flows to detritus, and net primary production. There is also evidence that the size (TST) or 'power' of each system decreased greatly between the focal periods. These changes were almost certainly attributed to the direct bottom up-effects of nutrient reductions which altered the abundance of benthic primary producers, with cascading consequences on invertebrate and waterbird species at higher trophic levels. These changes were also responsible for changes in secondary production and a number of higher level systems metrics. The effects are believable, not because of a statistically rigorous experimental design, but because the effect sizes are very large, and the altered biodiversity and ecological functioning are clearly different relative to the post management periods.

Associated with TST, the network characteristics of the Tamar and Eden ascendency (A), capacity (C) and overhead (O), all decreased considerably by the post-management periods. This is consistent with Ulanowicz's (1980;86) interpretation that nutrient perturbed systems can be defined by any increase in system ascendency that causes a rise in total system throughput (TST), that more than compensates for any fall in the mutual information content (e.g. A, C or O) of the system. In other words, the greater nutrient inputs tend to simulate a systems growth but despite its augmented activity, its organisation or structure is degraded.

Relative ascendency (A/C) was very similar between pre and post-management periods, suggesting that each system was able to accommodate (or resist) the large-scale changes in nutrient loading, primary production, and invertebrate biomass. When only the relative fluxes are concerned, the Tamar Estuary showed a decline of -1.19% in ascendency (A/C) relative to a larger change of -3.66% in internal Ai/Ci by the 2005 period, indicating a higher dependency of this system on connections to adjacent ecological and physical systems (e.g. the Western English Channel). In contrast, internal relative ascendency (Ai/Ci) remained relatively similar between the periods (+0.53%) in the Eden system, indicating that this system has maintained its activity without too much dependence on external system connections. As the degree to which environmental change is likely to influence ecosystem resilience will depend on metacommunity structure and connectance (Dunne *et al.,* 2002; Fung *et al.,* 2015), the (A/C) index could therefore be a suitable indicator to compare ecosystems of different sizes (e.g. Mann *et al.,* 1989, Baird *et al.,* 1991).

446 **Table 4** Summary of ecological and network statistics/indices for the Tamar and Eden estuarine
447 systems.

Estuary	Tamar			Eden		
Indices	**1990**	**1992**	**2005**	**1999**	**2015**	**Units**
Sum of all consumption (∑ C)	27416	27790	12254	26122	9386	t km^{-2} yr^{-1}
Sum of all respiratory flows (∑ R)	16474	16698	7373	15696	5648	t km^{-2} yr^{-1}
Sum of all flows into detritus (∑ FtD)	60403	6379	2982	5763	2121	t km^{-2} yr^{-1}
Sum of all production (∑ P)	11508	10863	7156	8560	3860	t km^{-2} yr^{-1}
Total system throughput (TST)	54675	55592	23464	50526	17957	t km^{-2} yr^{-1}
Total biomass (excluding detritus) (∑B)	2680	2617	1703	1926	958	t km^{-2} yr^{-1}
Total primary production/total biomass (PP/B)	2.320	2.036	2,774	1.74	1.88	-
Total primary production/total respiration (PP/R)	0.367	0.319	0.641	0.21	0.35	-
Ascendency (A)	77715	79561	29844	68252	23523	Flowbits
Capacity (Ca)	256513	273649	127706	294697	84797	Flowbits
Overhead (O)	178798	194088	97862	226445	108320	Flowbits
Relative ascendency (A/C)%	30.02	30.68	31.21	23.16	29.21	%
Internal ascendency (IA)	47448	48099	20390	45641	15763	Flowbits
Internal capacity (IC)	175004	189876	89455	193430	75478	Flowbits
Internal overhead (IO)	127556	141777	69066	147047	59715	Flowbits
Internal relative ascendency (Ai/Ci)%	27.08	26.54	23.42	23.32	23.85	%

448

449 **3.2 Cycling structure**

450 As making judgment about the trophic status of two entire ecosystems based on a few information
451 indices may seem precarious to some (Ulanowicz, 2004; Fath *et al.,* 2007), comparisons between the
452 Tamar and Eden ecosystems were supported by a broader analysis of the two networks. Support for
453 comparisons were made by considering the trophic structure and cycling pathways contained within
454 the two ecosystems. Because each trophic pathway is a series of interconnected cycles, stressors
455 occurring at any point will disrupt flow to higher levels (Voris *et al.,* 1980; Ulanowicz, 1983). We
456 would expect therefore, that systems with greater resistance to and resilience from nutrient stress
457 to be more complex, in the sense that they contain longer loops of connections that cycle at lower
458 frequencies. Conversely, systems under increased nutrient stress would possess fewer such cycles,
459 due to link disruptions, and each cycle would transfer less medium, particularly to higher trophic
460 levels (Baird & Ulanowicz, 1993). Indeed this is what the comparison shows: the cycles derived from
461 the Tamar and Eden systems were deficient both in number and length under high nutrient levels
462 consistent with hypothesis that systems with longer cycles and low proportions of cycling are
463 indications of less stressed systems.

464

Considering the magnitude of mineral and nutrient cycling within the Tamar system, Finns Index (CI) increased between both periods by ~10 & 30% respectively (Table 5), while the Predatory cycling index (PI) increased initially by 0.18% but then decreased by 0.59%. Together these changes point to a general increase in the detrital cycling process, but a fall in the predatory species contribution to these processes. Networks of cycled flows for the Tamar show that the total number of cycles in the system is sixteen, with these cycles distributed to varying degrees though three cycling nexuses (cycles having the same smallest transfer is called a nexus (Baird *et al.,*1991)).

Table 5 Cycle distributions of the Tamar and Eden systems

Distribution (%) of cycles per nexus	**Tamar**			**Eden**	
	1990	**1992**	**2005**	**1999**	**2015**
1	16.67	16.67	16.67	10	10
2	50	50	50	40	40
3	33.33	33.33	33.33	30	30
4	0	0	0	20	20
Number of cycles	16	16	16	10	10
Average path length (API)	2.681	2.716	2.945	2.82	2.90
Throughput cycled (including detritus)t km^{-2} yr^{-1}	1034	1014	984	1395	754
Throughput cycled (excluding detritus)t km^{-2} yr^{-1}	290	365	449.34	12.52	33.29
Throughput cycled (by detritus) %	72.76	66.06	93.4	99.02	95.52
Predatory cycling index (PI) % of throughput w/o detritus	0.68	0.86	0.27	0.03	0.24
Finn's cycling index (CI) % of total throughput	10.90	20.76	40.54	19.08	40.37

The API of associated cycles, and throughput of material cycled (including detritus) was fairly consistent across the study period (2.6-2.9 and 1034-984 t km^{-2} yr^{-1} respectively), indicating that flows of cycling were consistently occurring over short and fast loops. The percentage of material specifically cycled by the detritus compartment was also proportionately high (>72%), with increasing importance by the 2005 period (>93%).

In comparison with the Tamar, the cycling structure of the Eden estuary consisted of a total of ten cycles, distributed to varying degrees though four cycling nexuses (Table 5). The API of associated cycles, was fairly consistent between the study periods (2.8-2.9) specifying that flows of cycling were occurring over short and fast loops. The percentage of material specifically cycled by the detritus compartment was also proportionately very high (>95%), with around about a 4% shift towards non-detritus based cycling during the 2015 period. Indices representing the regulating and cycling of nutrients in a system (CI and PI) also increased during the 2015 period, suggesting greater system retentiveness and a greater proportion of material cycled across both higher and lower trophic levels (Odum, 1969). Both estuaries were found to recycle a large proportion of their material though short-fast cycles, with the majority of matter (e.g. carbon) being retained for approximately 2-3 cycles. The increasingly high CI index indicates both estuaries have a relatively simple cycling structure with both CI and API of a similar order as other estuaries with a legacy of nutrient contamination e.g. the Ythan Scotland (Baird & Ulanowicz, 199), with a study by Raffaelli (2011) also showing a similar increase in the CI index under a period of nutrient reduction.

3.3 A safe operational space

In addition to managing stocks and flows, environmental managers often need to know if a particular model projection (or policy option) will push the system being managed into a potentially unsafe state (i.e. whether a system will cross a critical threshold or tipping point). Thus, scientists and managers invested in considering a whole-systems approach may not be interested in the marginal changes of all species (Donohue *et al.,* 2013), but instead whether the system is capable of accommodating potential changes while retaining its capacity to function while remaining within its "safe-operating" space, and hence is resilient (Raffaelli, 2016). While it should be accepted that no single descriptor can fully accommodate the multifaceted nature of ecosystem resilience (Ulanowicz, 1992), one possible way to derive system-level measures of resilience, is to adopt a holistic systems approach rather than trying to measure the independent trajectories of several indicators. In particular, Ulanowicz (2011) has argued that the network metric, "ascendency," has a restricted set of values for real-world ecosystems, where a system lacking ascendency has neither the extent of activity nor the internal organization needed to function sustainably. By contrast, systems that are so tightly constrained and honed to a particular environment appear ''brittle'' (in the sense of Holling (1986)) are prone to collapse in the face of even minor novel disturbances (Ulanowicz *et al.,* 2009). Systems that endure lie somewhere between these extremes, with such networks falling within a "Window of Vitality" (Ulanowicz, 2005). Further, Zorach & Ulanowicz (2003) have demonstrated that such connections within the "Window of Vitality" can be adequately captured using the structural properties of networks. Thus by plotting such variables, scientists and managers can make *a priori* predictions about the preferential loss or reduction of stocks (e.g. species, populations, communities), against the effects on ecosystem functioning in relation to a "safe operating space" (Raffaelli, 2015; 2016). Such an approach also allows trade-offs between different network configurations that support different management and policy options be considered (e.g. under the impacts of different nutrient regimes). In this way different modelling scenarios or management choices can be assessed in a cost effective and canonical way, without the need to disturb natural ecosystems (Dunne & Williams, 2009).

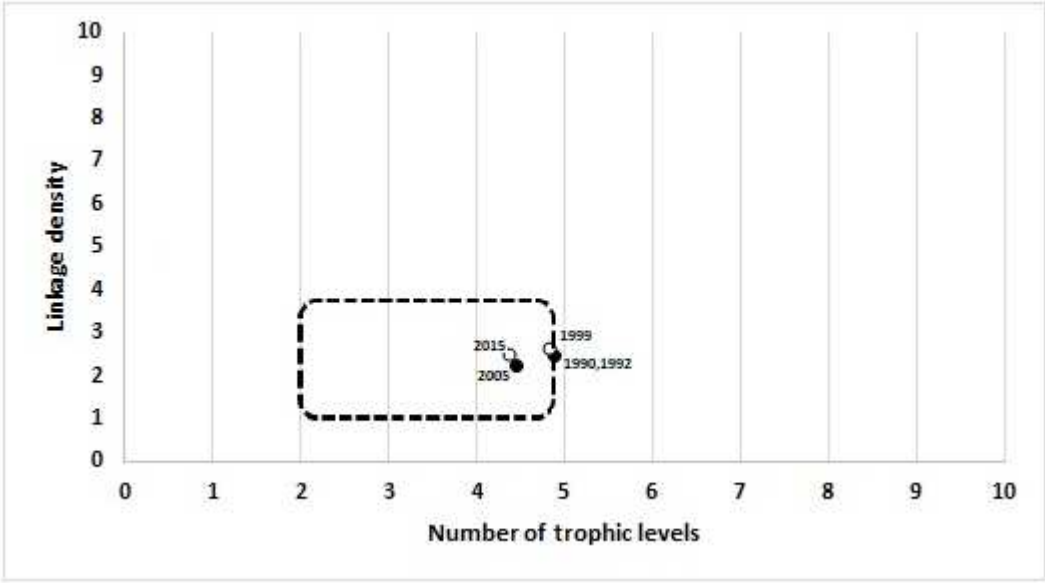

Figure 5 The "safe operating zone" (delineated by dotted lines) for the Tamar (Black circles) and Eden (White circles) estuaries defined by ascendency considerations and captured by two simple topological properties of food webs: linkage density and number of trophic levels.

Encompassing the changes in ascendency for the Tamar and Eden time periods within Ulanowicz's "Window of Vitality" (Figure 5), linkage density and number of trophic levels were shown to be very different between the pre- and post-management periods. This would locate the post-management Tamar and Eden periods within the right-hand boundary of the box in Figure 5. In contrast, during the high nutrient periods in both systems graduated towards the top right area of the perimeter space, with the Tamar effectively moving close to leaving the defined "safe operating zone". Under such circumstances, the results would indicate that the Eden system was able to accommodate historic large scales effects of changes in nutrient loading over the investigated periods, while the Tamar was operating in a relatively unsustainable state in the 1990's and relative to its less disturbed state in 2005. Implications for the Tamar in its high nutrient state would suggest that some trophic pathways may have narrowed, leaving the system less resilient with insufficient reserves to resist future disturbances (Ulanowicz, 2002). Subsequently both systems have moved closer to the geometric centre of the window (c = 1.25 and n = 3.25) which represents the best possible configuration for system sustainability (Ulanowicz *et al.,* 2009).

Overall, the system resilience measures used here suggest that large scale shifts in the nutrient balance of each estuary did not move the systems out of their safe space, which might give grounds for optimism of traditionally high nutrient systems such as estuaries (Leschine *et al.,* 2003; Elliott & Whitfield, 2011). Nonetheless, both versions of the Tamar and Eden networks were close to the "safe" operational boundary during the high nutrient periods and still remain just on the right of the Ulanowicz's ascendency curve, and at the top left corner of his "Window of Vitality". The question remains as to whether future stressors acting additively or synergistically with changes in nutrient loading (e.g. increased river flow or water temperatures) could push the systems out of their safe space. By plotting the values of the three variables related to Ulanowicz's (2005) "Window of Vitality" for many ecosystems under different environmental pressures, it may become possible to identify a region in perimeter space that characterises a generic healthy and robust ecosystem (Raffaelli, 2015).

3.4 Model limitations

When interpreting the modelled outputs from this study, several assumptions and limitations of model capability must be considered. Firstly, the development of an Ecopath model strongly depends on the quality of data used to build the model (Christensen & Walters, 2004). In this study, the data for almost all groups (Biomass, P/B, Q/B) were derived from site and time specific raw databases or stock specific assessments providing a solid background for dynamic modelling. However, for groups that play an important role in the Tamar or Eden estuaries food–web but for which no or very little data was available, i.e. certain macrofauna or meiofauna, their omission from the developed ecological networks may have led to an oversimplification in the structure of all food–web components. A specific lack of long term continuous biomass monitoring data in both case study areas, particularly for invertebrates and demersal fish, was also a specific limitation in validating historic trends and improving the validity of future predicted outcomes. Moreover, due to lack of specific knowledge, several functional groups have been aggregated, e.g. demersal fish potentially masking important species interactions (Essington, 2006). Other important factors that this study did not attempt to represent included the variability of future changing climate forcing/environmental or management regimes the adaptive potential of species (e.g. by affecting refuge and breeding space, altering animal behaviour, affecting hydrodynamic transports). While some of these uncertainties could be addressed by further laboratory experiments and *in situ* monitoring of ecosystem conditions, temporal variations in species-specific habitat factors, e.g. a loss of habitat, cannot be addressed in Ecopath but instead needs a spatial model (e.g. the Ecospace component of Ecopath with Ecosim, Christensen & Walters, 2004). We also acknowledge the need to raise the standards of Ecopath models in a management context (Heymans *et al.,* 2011; 2016), with similar standards needed in exploring ecosystem theory (Pocock *et al.,* 2016). Within the last few years, a growing number of diagnostic checks, including the PREBAL checks used in this paper, have been developed to establish best practices in creating and using such models (Mackinson *et al.,* 2009; Darwall *et al.,* 2010; Link, 2010; Heymans *et al.,* 2016; Scott *et al.,* 2016). These guidelines take into consideration the underlying thermodynamic and ecological rules available to users, recommend approaches to balance an Ecopath model, and how to evaluate uncertainty. In practice if these practices are upheld, it would allow not only more rigorous and consistent models, but would also aid in the acceptance of Ecopath and other mass balance models within science and management.

4 Conclusions

The process of constructing the Ecopath models here provides a valuable end product in itself through explicit synthesis of work from many researchers and has allowed a summarising of our current knowledge of the trophic flows, cycling structure and potential safe operational space of two estuaries with ongoing managing challenges associated with eutrophication. The models also help to highlight potential system specific data gaps (e.g. diet compositions, site-specific P/B, Q/B ratios, fish population numbers), that if collected in the future could be used to enhance and improve the knowledge of each system. The results of the mass balanced models show that the trophic structure, ecological functioning and general resilience of both the Tamer and Eden estuaries were affected similarly following distinct restoration events. This adds further evidence that reducing nutrient inputs to estuarine systems is not only beneficial to the biodiversity elements of a system (Howarth *et al.,* 2011), but also has wider positive implications on a wide range of important system properties which may only be revealed at the system level (Raffaelli, 2006). By understanding the recovery trajectory of individual systems and the metrics that can describe such responses, such information can be of direct relevance to many scientific and regulatory frameworks (Duarte *et al.,* 2015), for

example the European Water Framework Directive (WFD) in its pursuit to assess benthic integrity and determining good ecological status (GES). In the systems studied here, the shifts in the vast majority of the structural and functional indicators were generally consistent with recovery trajectories described for other UK and European Ecopath studies on nutrient disturbed systems (Patrício & Marques, 2006; Baeta *et al.,* 2011; Raffaelli, 2011; Selleslagh *et al.,* 2012). This supports the usefulness of ENA type approaches for assessing the recovery patterns of temperate transitional benthic systems. As scientists using the "Ecosystem Approach" are increasingly interested in how different impacts or recovery options will simultaneously change the ecological functioning of a system (Bennett, 2015) we also suggest that the comparison of information indices between networks when complemented by the inherent analysis of cycles can comprise a useful quantitative approach for inter-ecosystem comparisons (Wulff & Ulanowicz, 1989). Moreover, while the use of ENA modelling is extremely useful in establishing possible disturbance effects, one difficulty with the use of ecological models might be translating these results to stakeholders in an effective manner, (Fulton, 2011). As such, transforming process based models into simple graphical descriptions of risk may be useful to illustrate the integrity of the networks to future change. As coastal systems are host to a complex array of interactions between multiple stressors (Jackson *et al.,* 2016), a key next step will be to focus on the underlying processes and mechanisms whereby the stressors affecting these ecosystems interact.

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